Kinematics of chisel-tooth digging by African mole-rats

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Abstract

Mole-rats are known to use their protruding, chisel-like incisors to dig underground networks of tunnels, but it remains unknown how these incisors are used to break and displace the soil. Theoretically, different excavation strategies can be used. Mole-rats could either use their head depressor muscles to power scooping motions of the upper incisors (by nose-down head rotations) or the lower incisors (by nose-up head rotations), or their jaw adductors to grab and break the soil after penetrating both sets of incisors into the ground, or a combination of these mechanisms. To identify how chisel-tooth digging works, a kinematic analysis of this behaviour was performed based on high-speed videos of 19 individuals from the African mole-rat species *Fukomys micklemi* placed inside transparent tubes in a laboratory setting. Our analysis showed that the soil is penetrated by both the upper and lower incisors at a relatively high gape angle, generally with the head rotated nose-up. Initially, the upper incisors remain approximately stationary to function as an anchor to allow an upward movement of the lower incisors to grab the soil. Next, a quick, nose-down rotation of the head further detaches the soil and drops the soil below the head. Consequently, both jaw adduction and head depression are jointly used to power tooth-digging in *F. micklemi*. The same mechanism, but with longer digging cycles, and soil being thrown down at smaller gape sizes, was used when digging in harder soil.

Summary Statement

During digging, mole-rats anchor their upper incisors in the soil while the lower incisors are lifted through the soil. A quick, nose-down rotation of the head finishes an excavation cycle.

Introduction

Many rodents have become specialized for an underground lifestyle. At least 250 extant rodent species from six families spend most of their lives in self-constructed burrows (Begall et al. 2007). They construct these burrows either by scratching with their forelimbs, or by movements of their chisel-like incisors (e.g. Gasc et al. 1985). The latter behaviour is referred to as chisel-tooth digging. It has evolved independently at least once in each of the six extant families of subterranean and fossorial rodents (Stein 2000; McIntosh and Cox, 2016a). However, due to the technical difficulties with capture, keeping, breeding, and monitoring their behaviour (Begall et al. 2007), relatively little is known about the functional morphology and biomechanics of digging in these underground dwellers.

Mole-rats use their forward-pointing incisors to dig underground networks of tunnels (Jarvis and Sale, 1971). These bathyergid rodents extend their tunnels to run into plant roots or other geophytes for feeding (Robb et al., 2016), or to construct nest chambers (Jarvis et al., 1998). Several of their morphological features have been linked to digging: the capacity to open their mouth widely, lateral folds of the lips that almost entirely close the mouth at their widest gape to prevent the entry of soil (plate III B in Jarvis and Sale, 1971), large jaw adductor muscles to allow a forceful bite (Bekele, 1983a; Van Daele et al., 2009; Cox and Faulkes, 2014), valvular external nares to keep soil from entering the nasal cavities (Wake, 1993), and different aspects of their forelimbs to collect and sweep back loose soil (Jarvis and Sale, 1971).

However, how mole-rats use their incisors to break the soil remains largely unknown. A single study reported laboratory observations of digging behaviour in three species of mole-rats using transparent tubes (Jarvis and Sale, 1971): *Tachyoryctes* was described to dig with forward and upward sweeps of the lower incisors, *Heliophobius* and *Heterocephalus* were reported excavating the soil by biting at the soil face with their incisors. Unfortunately, these observations provide few insights on the mechanics of incisor-based digging. For example, force from the jaw adductors muscles may be used, but it could equally well be that head translations and rotations by the neck muscles are responsible for the digging motions.

In order to provide a theoretical framework to the study of tooth-digging, we identify four ways in which this type of digging could theoretically be performed (Fig. 1): (1) Mechanism A: the head is rotated nose-down by the head-depressor muscles in the neck, and the upper incisors penetrate the soil and scoop it downward (Fig. 1A). An engineering

analogue would be a classical backhoe excavator. (2) Mechanism B: the lower incisors are anchored in the soil while force from the jaw adductor muscles cause a downward movement of the upper incisors to scoop soil down. Activity of the head depressor muscles in the neck may assist this action (Fig. 1B). An engineering analogue would be a grab-digging machine (or grab dredger) where the lower part of the grabber experiences the most resistance to movement. (3) Mechanism C: the head is rotated nose-up by the head-elevator muscles in the neck, and the lower incisors penetrate the soil and scoop it upward (Fig. 1C). An analogue in machinery would be a front shovel excavator. (4) Mechanism D: the upper incisors are anchored in the soil while force from the jaw adductor muscles cause an elevation of the lower incisors to scoop soil up (Fig. 1D). This would resemble a grab-digging machine where the upper part of the grabber is stationary because it experiences more resistance than the lower part.

The mechanism employed by a mole-rat must be one of these four hypothetical mechanisms, or a combination thereof (excluding the combination of A with C) (Fig. 1). The observations by Jarvis and Sale (1971) for *Tachyoryctes* could fall either under mechanism C or D (Fig. 1 C,D). Those for *Heliophobius* and *Heterocephalus* probably fall either under mechanisms B or D (Fig. 1 B,D). On the other hand, the larger head elevator muscles (musculus semispinalis capitis and musculus splenius) in the mole-rat compared to a non-tooth-digging rodent, the black rat (*Rattus rattus*) (Bekele, 1983b), may suggest a role for mechanism C (Fig. 1C).

In the light of the above hypotheses, we test how digging is performed in a species that is specialised in using its incisors for this purpose: the African mole-rat, *Fukomys micklemi*. To do so, its digging kinematics will be analysed based on high-speed videography. This analysis will be the first to shed light on the role of the upper and lower incisors during digging, and provide indications on whether chisel-tooth digging is powered by jaw adduction, head depression or elevation, or both.

Additionally, we will test how the hardness of the soil affects digging kinematics. Since soil penetrability strongly depends on the local soil type and its present moisture level, mole-rats will inevitably be confronted with a wide variation in soil hardness in nature (Brett 1991). It was hypothesised that tooth digging allowed the exploitation of a broader range of soil types compared to (only) claw digging (Lessa and Thaeler, 1989). Previous studies showed that soil hardness has a profound influence on the digging metabolic rate, and on the

speed of tunnel extension in tooth-digging mole-rats (Lovegrove 1989; Brett 1991). As tooth wear by digging in hard surface crusts during the dry season is hypothesised to be costly (Brett 1991), maybe mole-rats modify their digging kinematics to minimise tooth wear in hard soils. A comparison between digging in soft and hard soil will allow us to evaluate whether *Fukomys micklemi* adjusts its digging kinematics in function of soil hardness.

Materials and Methods

Animals

The animals originate from an expedition in Southern Zambia (Sekute area) by P. Van Daele in September 2008, for which the Zambian Wildlife Authority provided the necessary permits (numbers 014508 and 009534). They belong to *Fukomys micklemi* Chubb (1909), more specifically the Sekute cytotype, 2n = 56 (Van Daele et al., 2004). Live specimens were transported to Belgium where they were kept in a climate-controlled chamber. The animals lived in constant darkness, except when they were fed and during the recording sessions. More detailed information on the composition, behaviour, and housing conditions of the colonies at Ghent University can be found in Desmet et al. (2014).

Experimental set-up

A transparent glass tube with a square cross-section (internal) of 6 x 6 cm was constructed. Rubber mats with a saw tooth profile were glued to the bottom side to provide grip. An open metal box (6 x 6 x 6 cm) containing the compressed soil was connected to one side of the tube. The size of this tube approaches the diameter of tunnels observed in the field for *F. micklemi*. Two LED arrays provided additional illumination at the digging scene. A JVC GZ-GX1 camera (JVC Kenwood, Yokohama, Japan) was placed with the lens axis parallel to the soil surface to film the digging mole-rat from a lateral view at 250 frames per second with a resolution of 720 x 288 pixels after deinterlacing.

To allow us to evaluate the effects of soil hardness on digging kinematics, soil samples of two different hardnesses were prepared: one type referred to as ‘soft soil’ consisted of fresh potting soil that was forcefully stamped into the metal container box. The ‘hard soil’ consisted of the same material, but first mixed with water (30 ml per 0.5 kg soil), stamped into the metal boxes, and baked for 18 hours at 55°C. Previous research on our colonies of *F. micklemi* showed that the mass of excavated soil per unit of time was significantly smaller in

the 18h baked soil compared to the unbaked soil (decrease by approximately 30%; Deschutter, 2011). This shows that the difference in hardness between our two soil samples is sufficient to cause a significant decrease in the speed of tunnel extension. According to measurements of soil penetration resistance using a laboratory-type, moving-tip penetrometer (T-5001 , J.J. Lloyd Instruments Ltd., Southampton, UK) at 2 mm per minute up to 10 mm of depth (Ghent University, Department of Soil Management), the penetration strength was approximately 0.1 kPa/mm for the soft soil and 0.5 kPa/mm for the hard soil.

High-speed videos were made of 19 individuals from 2 colonies of *F. micklemi*, 10 and 9 from each colony. From each individual 10 digging cycles were recorded, 5 in soft soil, 5 in hard soil. After a single recording, the animals were transferred back to their colony. Individuals were recognized by their unique pattern of spots on their dorsal side. These individuals were all adults and were randomly selected from the colony. The mean length (± standard deviation) of the head (upper incisor base to the centre of the ear in lateral-view images: between landmarks l1 and l3 in Fig. 2) was 28 ± 3 mm (range 23-35 mm). The animal handling protocols approved by the ethical committee of Ghent University were strictly followed.

Kinematic analysis

Only the video frames of the first soil-breaking movement cycle from a digging sequence were selected, since afterward the teeth could no longer be observed during digging. Small bites at the soil when the mole-rats were sensing the environment sometimes preceded this first true dig cycle, but these were not analysed. A small proportion of the videos were not used because the mole-rat rolled its head to perform a non-vertical bite at the soil. The position of 5 landmarks were quantified on each of these frames (Fig. 2) by manual digitisation to generate five kinematic profiles: (1) gape angle: the angle (< 180°) between the base of the upper incisor, the ear (which is close to the jaw joint; McIntosh and Cox, 2016b), and the base of the lower incisor; (2) cranium angle: the sharp angle between the line connecting the base of the upper incisors to a landmark on the back of the head, and the horizontal (positive angle = nose up; negative angle = nose-down); (3) neck angle: the angle between the upper incisor landmark, the landmark on the back of the head, and the landmark on the trunk (> 180° = head lifted above body axis); (4) upper incisor height: the vertical distance between the upper incisor base landmark and the horizontal ground surface; (5) lower

incisor height: the vertical distance between the lower incisor base landmark and the horizontal ground surface.

As *F. micklemi* does not have a pinna of the outer ear (Burda, 2006), the ear centre landmark (*3* in Fig. 2) will not shift because of pinna orientation. To validate whether the total distance along the upper and lower jaws (respectively landmarks *1* to *3* and *2* to *3* in Fig. 2) remains constant throughout a digging cycle (e.g. not being influenced by potential lip movement), we calculated the summed distance of *1* to *3* and *2* to *3* (Fig. 2), and found that the mean profile shows changes over time that are less than 5% of the mean. Taking into account the curvature of the incisors, such a shift of 5% in the distance from the ear landmark may affect gape distance by about 4%, and gape angle by about 9% for the gape angle displayed in Fig. 2. However, it is likely that part of this 5% shift in marker distance is caused by slight yaw movement of the head, which have a negligible effect on the calculated gape distance and gape angle. Consequently, effects of lip movement on the calculated kinematic profiles cannot be entirely excluded, but are estimated to be acceptably small given the purpose of our study. Finally, when the neck angle becomes larger (> 200°; neck angle as defined above), the dorsal skin will form a hump just posterior of the head. Landmark *4* (Fig. 2) on the posterior end of the head was always placed anterior to this hump to avoid effects of skin bulging on the calculated cranium and neck angles.

Digitization noise was reduced by applying a low-pass fourth-order zero phase-shift Butterworth filter (cut-off frequency of 30 Hz) to the raw data. The time was set at 0 when the gape reached a peak angle near the time the teeth first penetrated the soil. To describe the general patterns of motion for a multitude of digging sequences per individual and for multiple individuals, kinematic profiles were averaged after assigning a relative time scale (0% = maximum gape angle; 100% = minimum cranium angle). The latter procedure avoids averaging artefacts due to variation in duration between digging sequences.

Thirteen variables were calculated from these kinematic profiles (averaged profiles per individual and soil type) to describe the variation among digging sequences, and to statistically compare the kinematics of digging in hard and soft soil (both $N = 19$): (1) the maximum gape angle near the time of the teeth penetrating the soil, (2) minimum gape angle near the end of soil excavation, (3) time to minimum gape angle (in absolute time), (4) average speed of gape closing, (5) the maximum gape angle after the release of the soil from the mouth, (6) maximum cranium angle, (7) minimum cranium angle, (8) time between

maximum gape and minimum cranium angle (in absolute time), (9) average speed of nose-down rotation of the cranium, (10) vertical displacement of the upper incisors between t = 0 and t = 50%, (11) vertical displacement of the lower incisors in the interval t = 0% to 50%, (12) the vertical displacement of the upper incisors between t = 50% and t = 100%, (13) vertical displacement of the lower incisors in the time interval t = 50% to t = 100%. The latter four variables will allow us to evaluate the contribution of the upper and lower incisors to the digging work, and whether there is a difference between early (0% to 50%) and late (50% to 100%) in the digging cycle.

Statistics

All 13 variables did not show significant differences from being normally distributed according to the Anderson-Darling test ($P > 0.2$, $N = 19$), a powerful test to assess the assumption of normality for parametric statistical analysis (Razali and Wah, 2011). The variances between the two soil types did not differ significantly according to Bartlett tests. Next, a paired t-test (two-tailed) was performed to test for kinematic differences between the two types of soil. Statistic were performed using MaxStat 3.6 (MaxStat Software, Cleverns, Germany).

Results

General behaviour

Generally, at first encounter, the soil was sniffed by the mole-rats. Next, small-gape, exploratory bites at the soil were often observed. A sequence of digging cycles followed (supplementary video 1), of which the kinematics of the first cycle at large gape angle will be described in detail below. At variable intervals, the accumulating soil below the head was moved posteriorly by scooping with the forelimbs. In between the digging, the excavated soil was sometimes manipulated by the mole-rats, including breaking down of the larger pieces of soil by biting.

Digging kinematics

The sequence of motions during a digging cycle, illustrated by an example in Fig. 3, showed a general resemblance when comparing the kinematic profiles of digging in the soft and hard soil preparations in function of our relative time scale (Fig. 4). We first describe this

general pattern, followed by a description of the differences in kinematics between digging in the two soil types.

The digging cycle started by nose-up rotation of the cranium and opening of the mouth (Fig 3 A,B; Fig. 4 A-D from time -150 to 0%). On average (± s.d.), a cranium angle of 9 ± 5 degrees was reached (Fig. 4C,D; near time 0%), while the mouth opened to 71 ± 5 degrees (Fig. 4 A,B; near time 0%). Gape angle maxima frequently exceeded 80 degrees (30 out of the 190 cases), sometimes even 90 degrees (5 cases). The tips of the incisors were moved close to the soil, apparently without making contact to it. The neck angle profile (Fig. 4E,F) showed the same pattern as the cranium angle profile (Fig. C,D), and thus increased (up to 214 ± 10 degrees) until relative time 0% (time of maximum gape angle) when the cranium was rotated. Because of this strong resemblance between the profiles of neck angle and cranium angle, will we further only analyse the latter.

Near the instant of maximum gape, both incisors started penetrating the soil (Fig. 3C,D). During soil-penetration, the upper incisor showed relatively little downward movement (-1.8 ± 1.6 mm from time 0 to 50%; Fig. 4 G,H) compared to the upward movement of the lower incisors (5.6 ± 1.9 mm from time 0 to 50%; Fig. 4 I,J). During the time when the closing of the mouth slowed down (relative time about 50%) and the minimum gape was reached (relative time = 77 ± 13%), fast nose-down rotation of the cranium started (Fig. 4 C,D). The soil clamped between the upper and lower incisors was then brought down (Fig. 3E). Finally, the mouth opened again and the soil that hadn't already fallen before, was released (Fig. 3F). Preparing for the next digging cycle, the cranium was lifted again and mouth opening continued. The absolute time from the instant of maximum gape to the instant of minimum cranium angle was 0.22 ± 0.8 s, though this depended on the soil hardness (see below).

Kinematic differences in soft *versus* hard soil

Digging kinematics in compacted soil (referred to as soft soil) versus the compacted and 18 hours-baked soil (referred to as hard soil) differed in several aspects. While the statistical results are given in Table 1, the associated relative difference of hard versus soft soil digging are written below. The time between the instant of maximum gape and the instant of minimum cranium angle was significantly larger (+ 56% absolute time) when digging in hard soil versus soft soil. At the instant of releasing the soil, the minimum gape

angle was significantly smaller (-15%) in hard soil, and it took a significantly longer time for the mole-rats to close the mouth to this minimum gape angle (+77% absolute time). As a result, the speed of gape closing was significantly lower in hard soil (-25%). During the following nose-down head rotation phase, the cranium was rotated to a less steep inclination when feeding in hard versus soft soil (-31% cranium angle), at a significantly reduced speed (-53%). The associated downward movements of the incisors during this nose-down head tilting phase (relative time 50 to 100%) were also smaller in hard versus soft soil (-34 and 43% for, respectively, the upper and lower incisors). The other variables, namely the maximum gape angle, the maximum cranium angle, the maximum gape angle after the release of the soil, and the displacements of the incisors during the mouth-closing phase (relative time 0 to 50%), did not differ significantly between digging in two different types of soil. As the ratio of the standard deviation and the mean from Table 1 was higher for twelve of the thirteen analysed kinematic variables, our data suggest that inter-individual kinematic variability increased with soil hardness in *F. micklemi*.

Discussion

Fukomys micklemi mole-rats start digging with a biting phase during which the upper incisors are anchored in the soil while the lower incisors are elevated through the soil, followed by a phase of nose-down rotation of the head at an approximately constant gape (Figs. 3,4). From the four hypothetical mechanisms by which digging with the incisors could occur (Fig. 1), the initial biting phase corresponds to hypothetical digging mechanism D (i.e. biting with anchored upper incisors and elevating the lower incisors; Fig. 1D). Although the upper incisors aren't completely immobile during biting the soil (on average moving 1.8 mm down), the lower incisors move over a considerably longer distance up through the soil (on average more than 3 times the displacement of the upper incisors; Table 1). This means that the lower incisors do about ¾ of the excavating work during the biting phase, and the upper incisors about ¼.

The movement during the following nose-down head rotation phase resembles best the hypothetical mechanism A (i.e. upper incisor depression by nose-down torque about the neck joint; Fig. 1A). Yet, instead of the upper incisors scraping through the attached soil as described for this mechanism A, the soil that hasn't fallen down automatically by the foregoing upward scooping of the lower incisors is brought down while being clamped between the upper and lower incisors. Generally, after the biting phase, the grasped soil does

not seem to be entirely loose, especially for our harder, baked soil samples. Force from the neck powering the nose-down rotation of the head is thus actively contributing to the breaking down of the soil.

The observed change in neck angle during the nose-down head rotation phase, on average 94 ± 14 °, is large, but certainly not exceptional among mammals. For example, rabbits, guinea pigs, or cats already have ranges of motion of about 100 ° only at the atlanto-occipital articulation (i.e. the joint between the head and the first cervical vertebra; Graf et al. 1995). Active sagittal-plane ranges of motion of 125 ± 19 ° of the neck are known for humans (Reynolds et al. 2009). As the above examples are from species that do not dig with their head, this may suggest that no specific adaptations to the neck's range of motion are needed for tooth-digging. Yet, a sufficiently large rotational mobility of the head-neck allows the forelimbs and shoulder to remain fixed to be in a position to efficiently provide forward force during digging. This approximately immobile pectoral region (landmark *5* in Fig. 2) explains why the change in neck angle is about twice the change in cranium angle (Figs. 4C-F).

Our results suggest that the role of the upper and lower incisors during digging is different: the upper incisors are anchored into the soil, while the lower incisors move up to do most of the penetrating and soil-grasping work. Upward sweeps of the lower incisors to cut away soil are also described quantitatively in the literature for the spalacid *Tachyoryctes* (Jarvis and Sale, 1971). Consequently, the kinematics of the jaws during this part of the digging cycle seems to be similar in at least one other tooth-digging species, notably from a group of rodents (Spalacidae) that is distantly related from bathyergids like *Fukomys* (Blanga-Kanfi et al. 2009). This difference in function between the upper and lower incisors seems to be reflected in the mole-rat's anatomy, as the external protrusion of the lower incisors is larger than that of the upper incisors (Fig. 2). This anatomical difference indicates that the lower incisors are better suited for the excavation work than the upper incisors.

The current kinematic data are not sufficient to fully understand why the lower incisors are displaced considerably more through the soil than the upper incisors during digging. We initially expected that the incisors that experience the least resistive force from the soil to move the most. Apart from the local mechanical properties of the soil (which on average should be equal), this resistive force will be influenced by the penetration depth of the teeth into the soil, and by the angle at which upper incisors and lower incisors penetrate into

the soil. For neither of these two aspects, a lower resistive force can be predicted for the upper incisors: they are shorter and the penetration angles appear to be similar compared to the lower incisors (Fig. 2, 3B). Perhaps the lower jaw will inevitably follow a path of lower resistance when being forced into the soil due to its lower mass in combination with the flexibility of the jaw joint, which may automatically result in farther motion in the soil compared to the upper incisors. Alternatively, force from the head-elevator muscles during the biting phase could resist the downward movement of the upper incisors during biting. However, at first sight, it seems illogical that any action contributing to the excavation (i.e. downward movement of the upper incisors) would be actively resisted. Yet, the strategy to first firmly penetrate the lower incisors into the soil while maintaining a large gape (reducing travel of the upper incisors), would allow the mole-rats to follow this phase by a downward force on the firmly grabbed parcel of soil that can be very high since the jaw adductors and head depressor can then work in parallel to jointly produce nose-down torque on the cranium. In addition, the rotation of the cranium at this instant can give a high-leverage effect against the hard soil, similar to rotating a shovel after sticking it into the ground. Especially for digging in soil that is harder than the samples used in the current study, this strategy seems ideal to perform the final breaking of the most firmly attached soil parts.

However, electromyographic analyses (e.g. van der Leeuw et al. 2001; Herrel et al. 2008; Konow et al. 2011) seem required to fully unravel the role of the neck muscles during tooth-digging. Because of the complexity of the cervical system, the role of each of the fourteen neck muscles during tooth-digging remains unclear (Bekele, 1983b). Especially during the phase of lower jaw elevation, during which the upper incisors remain anchored in the soil (Fig. 3C-D), it would be interesting to test whether mole-rats actively support this anchoring by increased activity in the head elevator muscles (and inactive head depressor muscles). Without electromyographic data, we cannot distinguish whether the observed kinematic pattern (Fig. 4) results from interactions with the soil powered by pure biting (i.e. only jaw adductor activated), or whether neck muscles help to control the position of the head.

Interestingly, the different roles of the upper and lower incisors during digging seem reflected during feeding. In some of the videos of the current study, pieces of wood and rocky soil concretions are further explored by the mole-rats. Doing so, they firmly hold the object using both forepaws (on the side of the object) and the upper incisors (Supplementary video 2). The axis of the upper incisors points approximately perpendicular to the object's surface. The lower incisors are used to scrape the object. This suggests that also during the incisive

phase of feeding (i.e. gnawing), the upper incisors play a part in anchoring. This kinematic pattern is more general among rodents, as also during gnawing in hamsters (*Mesocricetus auratus*), the upper incisors assist the forepaws to fix the food while the lower incisors do scraping or chipping movements (Gorniak, 1977).

This study will also provide a basis for future functional and evolutionary morphology studies. These studies often rely on biomechanical modelling approaches, for which several assumptions on the *in-vivo* functioning of the digging system need to be made (e.g. Van Daele et al., 2009; Becerra et al., 2014; McIntosh and Cox 2016a,c). For example, the mean gape angle of *Fukomys* during digging from the current study has already been used in a study of the mechanical advantages of the jaw adductor muscles of bathyergid rodents (McIntosh and Cox 2016b). A recent computational modelling study compared the performance of the cranium of a tooth-digging with that of a scratch-digging bathyergid species during biting (McIntosh and Cox, 2016a). This type of study could be further optimised to better represent a case of digging based on the presented data. This may apply, for example, to the following aspects: (1) the loading on the protruding part of the upper incisor during digging is probably distributed over its entire ventrally facing side, (2) maximal forces can surpass those generated by the jaw adductors (adding forces from nose-down cranial rotation torque), (3) the orientation of these forces are determined by the interaction with the soil around the upper incisors (so not necessary opposite to the force on the lower incisors as assumed for biting in McIntosh and Cox, 2016a), and (4) loading on the cranium in contact with the vertebra seems important as well given the role of cranium depression (and also forward pushing of the cranium via the forelimbs). Such fine-tuning of biomechanical models may help us to further identify cranial adaptation for tooth-digging.

Although it is not the purpose of our study to explore the full behavioural repertoire of *Fukomys micklemi* digging in soils of the complete range of hardnesses or brittleness encountered in nature, our experiments with the two different types of soil samples probably show the most prominent effects of soil hardness on digging kinematics. Firstly, the time to complete a full digging cycle increased with soil hardness (Table 1). Most likely, this is a consequence of the higher resistance of the soil to penetration of the teeth and to breaking. Secondly, we observe that the mouth closed to a smaller gape during biting in the harder soil, and nose-down rotation of the cranium was reduced. As the harder, baked soil is also dryer and probably more brittle, generally a smaller volume is grasped between the incisors, as a larger part already fell to the ground upon penetration of the lower incisors. This smaller,

dryer part of soil can also be more easily released, which probably explains the smaller nose-down rotation in our hard soil samples (Table 1). There are no indications of kinematic adjustments in function of reducing tooth wear during digging in hard soil *versus* soft soil. Nevertheless, confirming the results from previous respirometer experiments (Lovegrove 1989; Brett, 1991), the considerably longer duration of a digging cycle in hard soil (more than 50% extra) suggests that the consequences of soil hardness on digging energetics are drastic. Individuals also tend to vary more from each other in relative amplitude and duration of their digging movements in harder soils, suggesting diverging individual preferences in how to deal with harder soils.

In conclusion, our quantification of the kinematics of tooth-digging by the bathyergid species *Fukomys micklemi* shows a dual-phase pattern: starting from a wide gape, first the elevating lower incisors grab the soil while the upper incisors mainly provide anchoring. Secondly, the grabbed soil is further detached and thrown down by nose-down head rotation. Both head depression and jaw adduction are thus involved in tooth-digging, with different roles for the upper incisors (anchoring function) and lower incisors (scraping and grabbing function). These new insights on the mechanics of tooth-digging will be important for future studies on the form, function and behaviour of the cranio-cervical system of rodents.

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Competing interests

No competing interests declared

Author contributions

Conceptualization: S.V.W., D.A.; Investigation: S.H.; Formal analysis: S.H., S.V.W.; Visualization and Writing - original draft preparation: S.V.W.; Writing - review and editing: S.V.W, D.A.

Data availability

All raw and processed kinematic data used in this study are currently made available to reviewers for download from a public OneDrive folder (https://onedrive.live.com/?id=BB381647D2C48FB7%21112&cid=BB381647D2C48FB7), and will be transferred to Dryad upon the acceptance of this article.

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Figure Legends:

Fig. 1: Four potential mechanisms of chisel-tooth digging. A legend for the arrows used in the schematics is given in the box at the top. Further explanation on the four hypothetical mechanisms (A-D) is given above each drawing, and in the main text.

Fig. 2: Five digitized anatomical landmarks. These landmarks are: *1*, base of the upper incisors (dorsal edge); *2*, base of the lower incisors (ventral edge); *3*, centre of the ear; *4*, posterior tip of the head (dorsal edge); *5*, trunk landmark at half a head length caudal to the head (dorsal edge). Scale bar, 3 cm.

Fig. 3: The motion sequence of a digging cycle. Video frames subsequently show the start of nose-up cranial rotation (A), reaching maximum gape (B), initial soil penetration by the incisors (C), mouth closing mainly by lifting of lower incisors (D), nose-down cranial rotation bringing the grasped soil parcel down (E), and release of the soil (F). The five digitised landmarks (see Fig. 2 for definitions) and the three angles calculated from the landmark coordinates are shown in line drawings below each frame (green = gape angle, orange = cranium angle, blue = neck angle). Scale bar, 3 cm.

Fig. 4: Per-individual mean kinematic profiles of digging and soft and hard soil. Soft-soil kinematics are displayed on the left, hard-soil kinematics on the right (both $n = 19$). The gray-shaded area denotes the plus-minus one standard deviation range. The line-drawings on the left illustrate the kinematic variables. Note that the time-scale is relative (0 % = time of maximum gape shown by the vertical line, 100% = time of minimum cranium angle; both events are indicated by arrows), and a scale-bar for absolute time is given at the bottom.

Table 1: Comparison of kinematic variables from biting in soft versus harder soil

	soil type		
variable	Soft (mean ± s.d.; *n* = 19)	Hard (mean ± s.d.; *n* = 19)	*P* (paired t-test)*
Maximum gape angle (°)	72 ± 4	71 ± 6	0.33
Minimum gape angle (°)	50 ± 4	42 ± 4	**0.0000023**
Time to minimum gape angle (s)	0.13 ± 0.05	0.22 ± 0.10	**0.000096**
Average speed of gape closing (10^3 °/s)	0.20 ± 0.07	0.15 ± 0.05	**0.00045**
Maximum gape after soil release (°)	66 ± 5	66 ± 5	0.81
Maximum cranium angle (°)	10 ± 5	8 ± 6	0.073
Minimum cranium angle (°)	-36 ± 8	-25 ± 11	**0.000011**
Time to minimum cranium angle (s)	0.17 ± 0.05	0.27 ± 0.08	**0.000039**
Average speed of nose-down cranium rotation (10^3 °/s)	0.29 ± 0.08	0.13 ± 0.06	**0.00000003**
Upper incisor displacement from time 0 to 50% (mm)	-1.6 ± 1.8	-2.0 ± 1.4	0.48
Lower incisor displacement from time 0 to 50% (mm)	6.0 ± 1.8	5.5 ± 2.0	0.37
Upper incisor displacement from time 50 to 100% (mm)	-18 ± 4	-12 ± 5	**0.00002**
Lower incisor displacement from time 50 to 100% (mm)	-8 ± 3	-4 ± 4	**0.0048**

* *P*-values below the critical 0.05 are printed in bold

= output motion of the digging element

joint: = craniovertebral, = craniomandibular

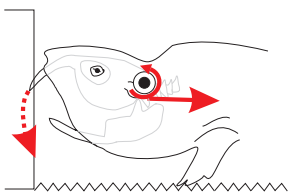
= main input force causing main torque or on moving element

= potentially assisting force causing torque on moving element

= required force transmission to digging element

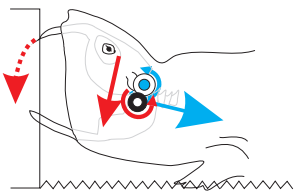
A

hypothetical mechanism A:
upper incisor depression
by nose-down torque
from neck muscles



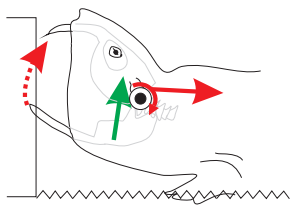
B

hypothetical mechanism B:
biting with anchored
lower incisors and
depressing upper incisors



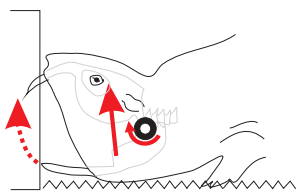
C

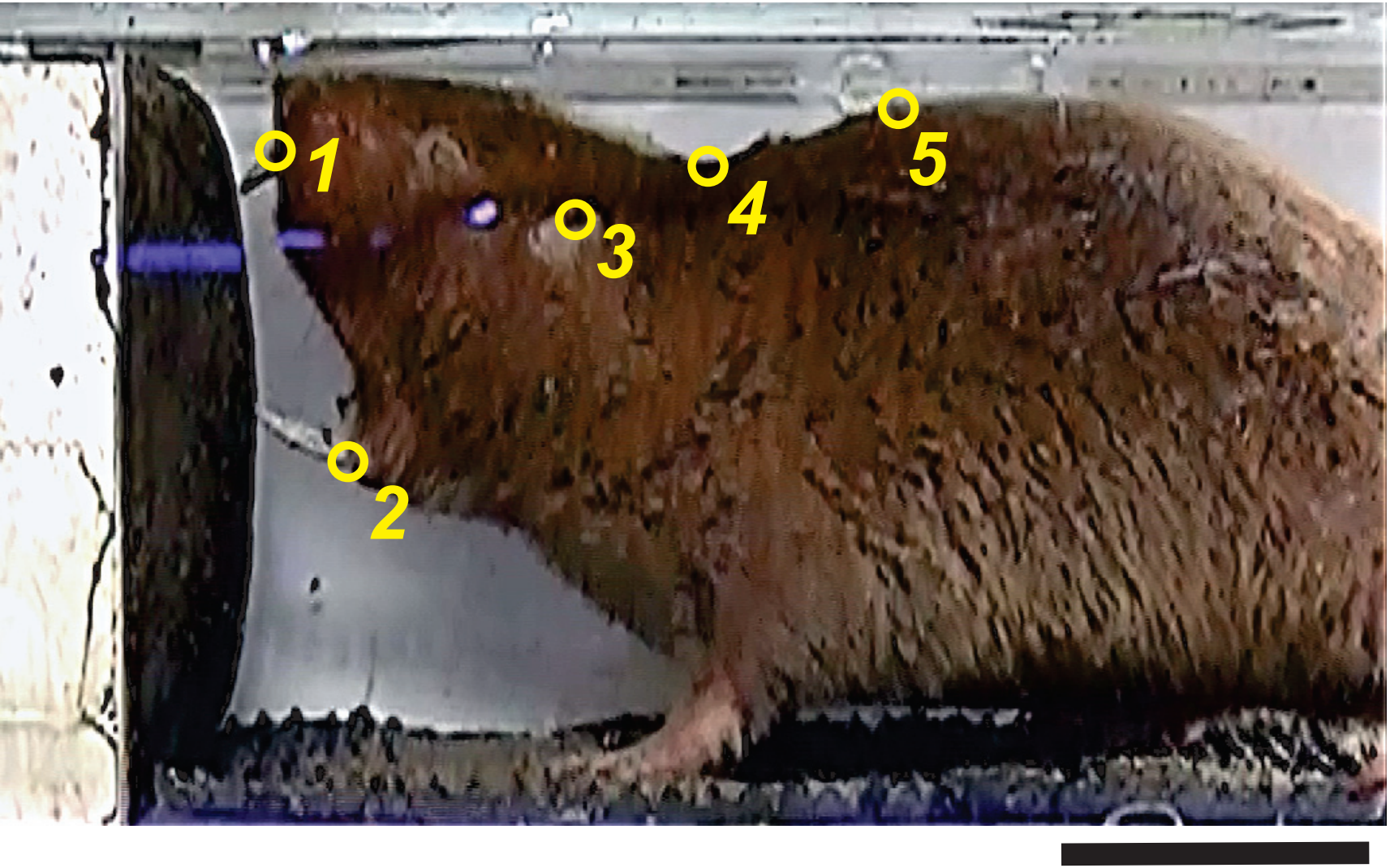
hypothetical mechanism C:
lower incisor elevation
by nose-up torque from
neck muscles

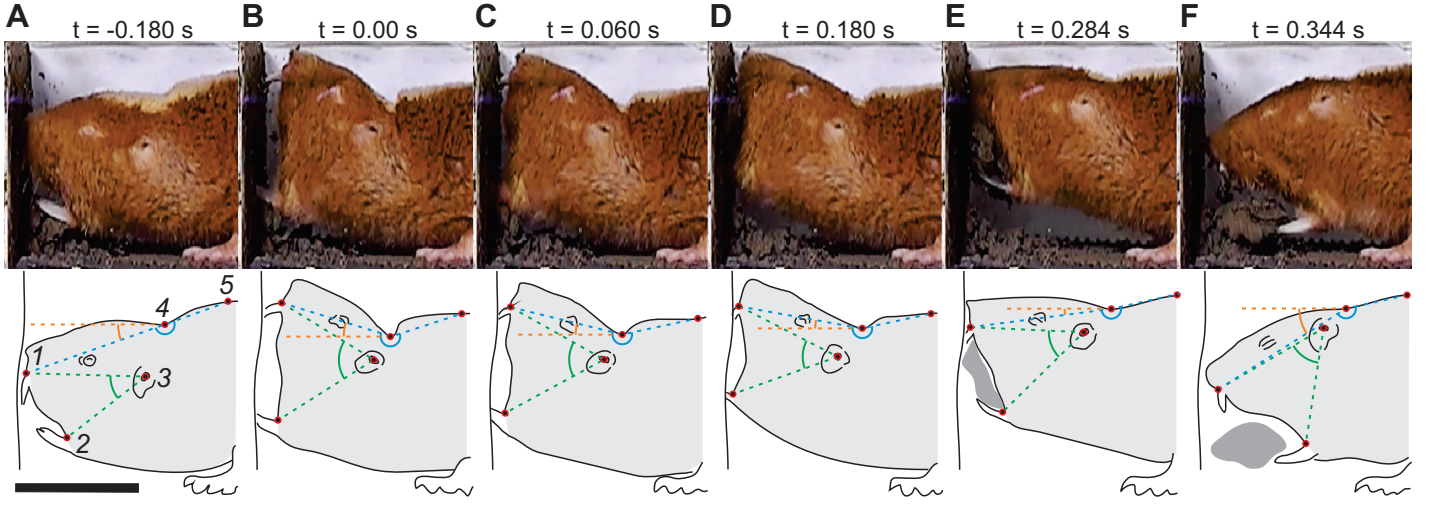


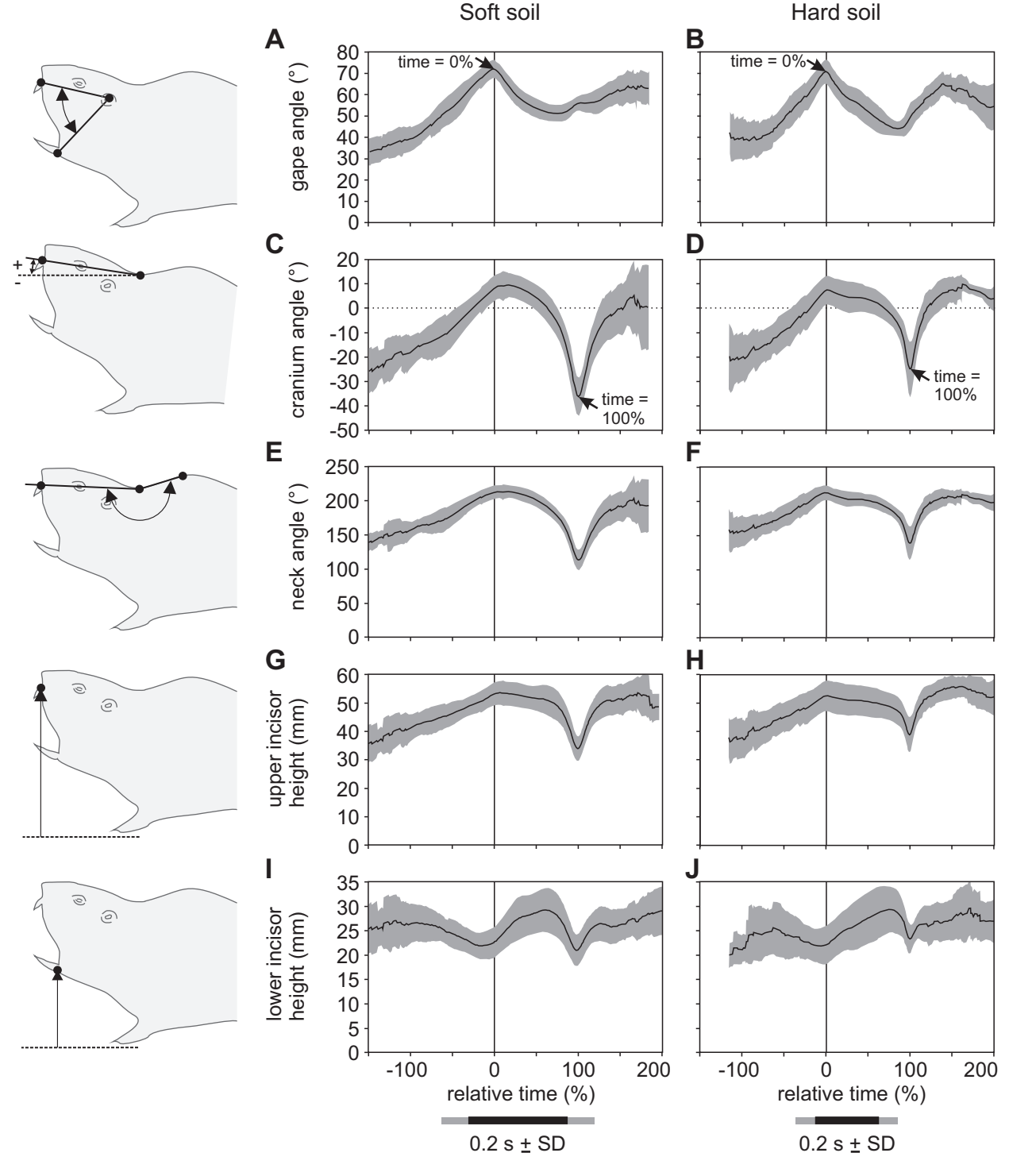
D

hypothetical mechanism D:
biting with anchored
upper incisors and
elevating lower incisors




1
2
3
4
5


A
t = -0.180 s
B
t = 0.00 s
C
t = 0.060 s
D
t = 0.180 s
E
t = 0.284 s
F
t = 0.344 s
1
2
3
4
5


Soft soil
Hard soil
A
B
C
D
E
F
G
H
I
J
gape angle (°)
cranium angle (°)
neck angle (°)
upper incisor height (mm)
lower incisor height (mm)
time = 0%
time = 100%
+
-
relative time (%)
0.2 s ± SD